The role of hand dominance and sensorimotor congruence in voluntary movement

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Abstract

The present study evaluated the neural changes due to effector use (unimanual left, unimanual right, bimanual) and visuomotor conflict induced by mirror-reversed vision during drawing behaviour. EEG phase synchronization, expressing interregional communication, showed that visuomotor incongruence perturbed information processing in both hemispheres. Furthermore, it was observed that the left hemisphere became temporally dominant when movements were executed with visuomotor conflict, independent of the performing hand(s). This observation emphasizes the superiority of the left hemisphere to control complex movements. In addition, the functional interactions between the hemispheres were also perturbed due to visuomotor discordance, indicating the crucial role of interhemispheric communication for movement control. These results highlight that functional connectivity patterns provide higher-order coding mechanisms of information processing. The data further underline the significance of the left hemisphere for intricate visuomotor skills.

Keywords: EEG, functional connectivity, phase synchronization

Introduction

Manual performance is strongly determined by hand dominance, especially in right-handers. In particular, in single-handed tasks, the preferred hand provides an enhanced performance as compared to the non-preferred hand (Peters 1980; Sainburg 2002) and is also less disturbed by perturbations such as visual illusions (Gonzalez et al. 2006). The well-defined factor of hand dominance is also noticed in bimanual assignments during which the preferred limb exerts a stronger influence on the non-preferred limb than vice versa (Byblow et al. 1999; de Poel et al. 2007). Together, these results point to the behavioural significance of the preferred hand for motor acts. From a neural point of view, it is recognized that a distributed network underlies manual performance. However, the hemispheric involvement varies as a function of the performing effector (Haaland et al. 2004). In particular, the left hemisphere is strongly linked with right hand and bimanual movements, whereas the right hemisphere is mostly associated with left hand movements (Serrien 2009). Then again, it has also been observed that several motion-related factors such as complexity and praxis are primarily represented in the left hemisphere (Frey 2008; Haaland et al. 2004; Wyke 1971). Accordingly, the premise has been acknowledged that hemispheric organization is distinct for movement control, with a pronounced dominance of the left hemisphere. In contrast to this notion, robust evidence is available that the right hemisphere is markedly involved in various spatial functions such as monitoring (Fink et al. 1999; Marshall and Fink 2001). The latter becomes especially evident in conflict situations such as during the exposure to environments in which the information from the visual and proprioceptive signals diverge. One such example is mirror drawing in which visual input about the target is mirror-reversed with respect to the hand motion (Lajoie et al. 1992; Miall and Cole 2007).

Considering the existing lateralization of function, it is relevant to take into account specialized processing of the right as well as left hemisphere in view of motor activities. In addition, it is important to consider the dynamic gating of information between both hemispheres, as each side will contribute in a specific manner to support skilled behaviour (Serrien et al. 2006; Stephan et al. 2007). Based on the previous arguments, it is reasoned that evaluating changes in hemispheric information processing as a function of the task

constraints will provide valuable insights into brain regulation. To examine this issue, the present experiment evaluated the performance of a visuomotor task with either hand (preferred vs. non-preferred) or both hands in a normal and sensorimotor conflict (mirror-reversed) situation. The hypothesis was that the experimental factors of effector (left, right, both) and sensorimotor conflict would distinctively modify the degree of information processing across both hemispheres. Data analysis using established EEG techniques focused on functional connectivity profiles in the frequency domain. In this respect, this concept of functional connectivity characterizes the concurrent activity of remote brain regions and is commonly measured through patterns of synchronization at various neural sites. The notion is based on the hypothesis that functional coupling of neural activity offers a means to process and integrate task-related information with respect to skilled behaviour.

Materials and Method

Subjects

Ten right-handed individuals (age: 22.5±6.3 years) as determined by the Edinburgh handedness inventory (Oldfield 1971) participated in the experiment. In accordance with the declaration of Helsinki, the subjects gave informed consent to take part in the study, which was approved by the local ethics committee.

Tasks and procedure

The participants were asked to perform continuous drawing movements with the right (preferred) hand, left (non-preferred) hand or with both hands. Each individual drawing consisted of a triangle of which each segment involved a path length of 10 cm and a line width of 8 mm. The drawing tasks were executed under 2 experimental conditions; with normal vision (control) and with mirror-inverted vision. Both conditions involved patterns with similar kinematics. Subjects first performed the control followed by the mirror conditions. The order within the control and within the mirror conditions was counterbalanced (i.e., order of performing effector). Each individual drawing was performed on a separate Wacom writing tablet, using an ink- and wireless pen (tip diameter = 1 mm).

The pen trajectories were acquired in x- and y-coordinates by using E-Prime software (Psychology Software Tools Inc., Pittsburgh, USA). For each individual drawing, the triangle model was placed behind the respective writing tablet, and accordingly required the participants to perform a model copying task. In the mirror-reversed condition, a mirror with semi-silvered coated properties was placed between the model(s) and tablet(s), enabling mirror-reflected image(s) to be drawn. The start position/direction of the drawings was indicated to the subjects, and the instructions were to draw continuously for the duration of the trial, as fast and as accurately as possible. Trials lasted 35 s each, and there were 2 trials per task condition. Practice with and without the mirror was provided. There were small breaks in between trials. As an estimate of behavioural performance, path velocity of the trajectories was determined for each subject and task condition. Moreover, path length was calculated as the total Euclidean distance over all collected data points as a function of trial duration.

EEG recordings and analysis

Continuous EEG was recorded using the Electrical Geodesics Inc. 128-channel system. EEG signals were amplified, band-pass filtered 0.05 Hz–100 Hz, and sampled at 250 Hz with a vertex reference. Data pre-processing was carried out using BESA software (MEGIS Software GmbH, Gräfelfing, Germany), and epochs contaminated by artifacts such as eye movements and EMG-related activity were corrected for using its algorithm. A reference-free montage was subsequently adopted for further analysis using the EEGLAB Matlab Toolbox (Delorme and Makeig 2004). The trials were segmented into epochs of 800 ms (with an overlap of 300 ms with previous and subsequent epoch for smoothing purposes, excluding the first and last epoch) and subjected to a threshold-based rejection of epochs, resulting in an average of 114 epochs per subject and task condition. A wavelet analysis extracted time–frequency complex phases using three cycles at frequencies in the low beta band (13-21 Hz), based on earlier work of visuomotor behaviour (Classen et al. 1998). A sliding window of 260 ms was used with a frequency resolution of 1 Hz. Thereafter, phase synchronization was calculated as an estimate of functional connectivity in the frequency domain. It was determined for all specified time points and frequencies,

and subsequently averaged for each subject and task condition. As a measurement of coupling between two signals at any given frequency, phase synchronization varies between 0 (no correlation) and 1 (perfect correlation). To describe cortical activity, a region of interest approach was adopted that focused on a restricted number of electrodes. The electrodes were selected based on earlier EEG studies (Classen et al. 1998; Hummel et al. 2003; Serrien 2009) and were estimated to overlie prefrontal, premotor, sensorimotor, parietal and occipital areas. The division of electrodes resulted in the following connectivity groupings: intrahemispheric left (F3-FC3, F3-C3, F3-CP3, F3-P3, F3-O1, FC3-C3, FC3-CP3, FC3-P3, FC3-O1, C3-CP3, C3-P3, C3-O1, CP3-P3, CP3-O1, P3-O1), intrahemispheric right (F4-FC4, F4-C4, F4-CP4, F4-P4, F4-O2, FC4-C4, FC4-CP4, FC4-P4, FC4-O2, C4-CP4, C4-P4, C4-O2, CP4-P4, CP4-O2, P4-O2), interhemispheric (F3-F4, FC3-FC4, C3-C4, CP3-CP4, P3-P4, O1-O2) and midline (FCz-CPz), (Serrien 2009). Before statistical operations were conducted, scores were transformed using the inverse hyperbolic tangent to stabilize variances. All the processed data were analyzed using Statistica software (StatSoft Inc., Tulsa, USA). Adjustments were made in case of violation of the sphericity assumption by using the Greenhouse–Geisser procedure. Post-hoc testing included Tukey's procedure for multiple comparisons.

Results

The EEG phase synchronization data were analyzed separately for intrahemispheric (left and right), interhemispheric and midline couplings. The main analyses involved 2 x 3 x 2 ANOVAs on sensorimotor conflict (no mirror, with mirror), effector (left hand, right hand, bimanual), and hemisphere (left hemisphere, right hemisphere). *For intrahemispheric connectivity*, the ANOVA showed a significant main effect of sensorimotor conflict [$F(1,9)=6.07$, $P<0.04$], with no mirror (control) movements showing stronger coupling than mirror movements. The sensorimotor conflict x effector x hemisphere interaction was also significant [$F(2,18)=4.76$, $P<0.02$]. Fig. 1A illustrates reduced coupling in the mirror compared to the no mirror tasks, with a stronger impact on the right than left hemisphere. Furthermore, the left hemisphere was influential for right hand performances in the no mirror condition and across all effector movements in the mirror condition. This result hints

at distinct hemispheric changes when effectors move in sensorimotor conflict situations. The latter was supported by examining the ratio of left vs. right hemisphere activation, which provides an indication about hemispheric balance. The ratio analyzed by means of a 2 x 3 ANOVA on sensorimotor conflict (no mirror, with mirror), effector (left hand, right hand, bimanual) revealed a significant sensorimotor conflict x effector interaction [$F(2,18)=4.50$, $P<0.02$). Fig. 1B illustrates that the left hemisphere which was prominent during all right hand movements (control and conflict conditions) became also temporally dominant for the other motor tasks (left hand and bimanual) when sensorimotor conflict was introduced.

Insert Fig. 1 about here

For interhemispheric connectivity, the ANOVA demonstrated a significant main effect of sensorimotor conflict [$F(1,9)=17.17$, $P<0.01$], with no mirror movements comprising stronger coupling than mirror movements. The sensorimotor conflict x effector interaction was significant [$F(2,18)=4.18$, $P<0.03$]. Fig. 2 indicates that in the no mirror condition, left hand movements induced greater coupling than right hand or bimanual movements ($P<0.05$), whereas synchronization differences between the moving effectors disappeared in the mirror condition.

Insert Fig. 2 about here

For midline connectivity, the ANOVA revealed a significant main effect of effector [$F(2,18)=4.32$, $P<0.03$], with bimanual movements evoking increased coupling as compared to unimanual movements ($P<0.05$). The mean scores of the no mirror and mirror conditions were .379±.015 and .371±.019 (left hand), .374±.016 and .372±.014 (right hand), .404±.017 and .400±.016 (bimanual).

The behavioural data of path velocity were analyzed by means of a 2 x 2 x 2 ANOVA on sensorimotor conflict (no mirror, with mirror), task (unimanual, bimanual), and hand (left hand, right hand). The analysis showed a significant main effect of sensorimotor

conflict [$F(1,9)=24.64$, $P<0.01$], task [$F(1,9)=76.66$, $P<0.01$], and hand [$F(1,9)=8.59$, $P<0.01$], with higher velocity scores being attained during no mirror than mirror conditions, unimanual than bimanual tasks, and right hand than left hand movements. The mean scores of the no mirror and mirror conditions in pixels/s (± coefficient of variation) were 277±5% and 162±11% (unimanual left), 287±7% and 179±12% (unimanual right), 202±14% and 110±9% (bimanual left), 204±11% and 119±7% (bimanual right).

Discussion

Neural information processing relies on principles of local (specialized) and global (distributed) control (Friston 2001). Whereas local processing denotes that certain functions engage segregated brain areas, distributed regulation implies that multifaceted functions depend on collective information processing from various regions (Tononi et al. 1998). Considering the intricate nature of typical behaviour, the argument can be made that its performance requires neural dynamics with interregional communication within and between hemispheres (Serrien et al. 2006; Stephan et al. 2007). To address this issue, research work has focused on functional connectivity profiles that capture the dynamic flow of information processing among widespread brain regions. In particular, synchronous oscillations have been proposed as a mechanism for coordinating neural processing across distributed areas (Varela et al. 2001).

In the present study, hemispheric information processing was examined during motor activities that required copying from model to drawing space. This behaviour imposed an implicit association between model and trajectory, and accordingly involved distinctive visuomotor transformations for successful task performance (Averbeck et al. 2003). Therefore, it is hypothesized that the task constraints of copying influenced the sensory weighting and performance strategies (i.e., shifts between model and trajectory), especially during visuomotor incongruence when the reference frames between eyes and hand(s) became incompatible. Besides the experimental manipulation of sensorimotor correspondence, which integrated discordant visual and proprioceptive information processing, drawing behaviour was assessed as a function of the performing effector (unimanual left, unimanual right, bimanual). It was anticipated that both factors

(sensorimotor conflict and performing effector) would influence distinctively the functional activation patterns associated with the drawing tasks, which normally engage distributed brain regions (Haaland and Delaney 1981; Makuuchi et al. 2003; Wyke 1971). Moreover, the argument was made that the neural dynamics associated with the motor tasks would adapt in response to the particular task constraints.

The EEG data revealed that intrahemispheric coupling in the low beta frequency band changed due to both experimental factors. *First*, visuomotor incongruence affected information processing in both hemispheres. This observation is in line with results from sensorimotor adaptation, which implicates the involvement from distributed regions (e.g., Contreras-Vidal et al. 2004; Inoue et al. 2000). Here, it is argued that interrupted visuoproprioceptive processing occurred in the right hemisphere (Lajoie et al. 1992; Weiss et al. 2006) while disrupted sensorimotor planning emerged in the left hemisphere (Miall and Cole 2007). Besides the modified intrahemispheric connectivity, the functional communication between the hemispheres was also perturbed due to visuomotor discordance, which underscores that interhemispheric interactions are crucial for movement regulation (Wahl et al. 2007). Furthermore, the no mirror vs. mirror effect was strongest for the left hand movements, which emphasizes an effect of hand dominance. This observation is likely related to a shift in hemispheric control when performing left hand movements in a visuomotor conflict condition (as discussed next). It further suggests an interhemispheric mechanism that integrates distinct pathways depending on the current neural dynamics.

Second, the effector used in the drawing activity modulated the intrahemispheric activation patterns. In particular, in the control (no mirror) conditions, the contralateral hemisphere was most dominant for the unimanual actions, whereas a similar degree of hemispheric activation was noted for the bimanual performances. However, these hemispheric differences changed when the drawing tasks were executed in the presence of visuomotor conflict. In this particular situation, the left hemisphere became temporally dominant, independent of the performing effector(s). This finding extends the superiority of the left hemisphere for controlling complex sequential movements (Haaland et al. 2004; Verstynen et al. 2005) with respect to intricate spatial skills. In the present context, this

left-sided dominance may associate with the integration of spatial and temporal information (Assmus et al. 2005) and/or visuomotor processing (Fisk and Goodale 1988; Gonzalez et al. 2006). That the functional balance between both hemispheres changed due to visuomotor incongruence suggests that hemispheric cooperation is essential for behavioural functioning. Furthermore, the present data also revealed that mesial connectivity was not affected by the sensory conflict situation, but was by the bimanual nature of the task constraints. The latter is in line with previous results that have shown that midline areas are important for coordinated acts (Serrien et al. 2002).

The results from the intra- and interhemispheric connectivity profiles have provided evidence that defined neural changes occur due to situations of sensorimotor incongruence in relation to the performing effector(s). These modifications hint at dynamic adjustments across the neural network for coping with the current task constraints. From a behavioural point of view, the results showed that execution slowed down when the task demands increased, i.e., performance in the presence of visuomotor conflict, left (non-preferred) hand as compared to right (preferred) hand movements, and bimanual in comparison to unimanual actions. Together, these situations likely evoked increased supervision of the task requirements.

In conclusion, everyday tasks often require skilled behaviour with either or both hands. Usually, these activities involve neural processing across distributed brain regions. In challenging conditions, neural regulation may be modified and accordingly have an impact on motor output. In the present study, it was shown that visuomotor incongruence and performing effector modulated interregional interactions. Furthermore, the findings indicated that the left hemisphere became influential when movements were executed with visuomotor conflict, independent of the hand(s) used. Accordingly, these data underline the superiority of the left hemisphere to control complex skills.

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Figure Caption

Fig. 1 (A) Intrahemispheric (left and right) coupling as a function of sensorimotor conflict (no mirror, with mirror) and performing effector (left hand, right hand, bimanual). (B) Ratio of left vs. right hemisphere activation associated with sensorimotor incongruence and effector used. The means ± SE are illustrated.

Fig. 2 Interhemispheric connectivity caused by sensorimotor conflict (no mirror, with mirror) and performing effector (left hand, right hand, bimanual). The means ± SE are illustrated.

References

Assmus A, Marshall JC, Noth J, Zilles K, Fink GR (2005) Difficulty of perceptual spatiotemporal integration modulates the neural activity of left inferior parietal cortex. Neurosci 132:923-927

Averbeck BB, Chafee MV, Crowe DA, Georgopoulos AP (2003) Neural activity in prefrontal cortex during copying geometrical shapes. I. Single cells encode shape, sequence, and metric parameters. Exp Brain Res 150:127–141

Byblow WD, Summers JJ, Semjen A, Wuyts IJ, Carson RG (1999) Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. Motor Control 3:372-393

Classen J, Gerloff C, Honda M, Hallett M (1998) Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. J Neurophysiol 79:1567-1573

Contreras-Vidal JL, Kerick SE (2004) Independent component analysis of dynamic brain responses during visuomotor adaptation. Neuroimage 21:936-945

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods 134:9-21

de Poel HJ, Peper CL, Beek PJ (2007) Handedness-related asymmetry in coupling strength in bimanual coordination: furthering theory and evidence. Acta Psychol 124:209-237

Fink GR, Marshall JC, Halligan PW, Frith CD, Driver J, Frackowiack RSJ, Dolan RJ (1999) The neural consequences of conflict between intention and the senses. Brain 122: 497-512

Fisk JD, Goodale MA (1988) The effects of unilateral brain damage on visually guided reaching: hemispheric differences in the nature of the deficit. Exp Brain Res 72:425-435

Frey SH (2008) Tool use, communicative gesture and cerebral asymmetries in the modern human brain. Philos Trans R Soc Lond B Biol Sci 363:1951-1957

Friston KJ (2001) Brain function, nonlinear coupling, and neuronal transients. Neuroscientist 7:406-418

Gonzalez CL, Ganel T, Goodale MA (2006) Hemispheric specialization for the visual control of action is independent of handedness. J Neurophysiol 95:3496-3501

Haaland KY, Delaney HD (1981) Motor deficits after left or right hemisphere damage due to stroke or tumor. Neuropsychologia 19:17-27

Haaland KY, Elsinger CL, Mayer AR, Durgerian S, Rao SM (2004) Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. J Cogn Neurosci 16:621-636

Hummel F, Kirsammer R, Gerloff C (2003) Ipsilateral cortical activation during finger sequences of increasing complexity: representation of movement difficulty or memory load? Clin Neurophysiol 114:605-613

Inoue K, Kawashima R, Satoh K, Kinomura S, Sugiura M, Goto R, Ito M, Fukuda H (2000) A pet study of visuomotor learning under optical rotation. Neuroimage 11:505-516

Lajoie Y, Paillard J, Teasdale N, Bard C, Fleury M, Forget R, Lamarre Y (1992) Mirror drawing in a deafferented patient and normal subjects: visuoproprioceptive conflict. Neurology 42:1104-1106

Makuuchi M, Kaminaga T, Sugishita M (2003) Both parietal lobes are involved in drawing: a functional mri study and implications for constructional apraxia. Brain Research: Cogn Brain Res 16:338-347

Marshall JC, Fink GR (2001) Spatial cognition: where we were and where we are. Neuroimage 14:S2-7

Miall RC, Cole J (2007) Evidence for stronger visuo-motor than visuo-proprioceptive conflict during mirror drawing performed by a deafferented subject and control subjects. Exp Brain Res 176:432-439

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97-113

Peters M (1980) Why the preferred hand taps more quickly than the non-preferred hand: Three experiments on handedness. Can J Psychol 34:62-71

Sainburg RL (2002) Evidence for a dynamic dominance hypothesis of handedness. Exp Brain Res 142:241-258

Serrien DJ (2009) Functional connectivity patterns during motor behaviour: The impact of past on present activity. Hum Brain Mapp 30:523-531

Serrien DJ, Ivry RB, Swinnen SP (2006) Dynamics of hemispheric specialization and integration in the context of motor control. Nat Rev Neurosci 7:160-166

Serrien DJ, Strens LH, Oliviero A, Brown P (2002) Repetitive transcranial magnetic stimulation of the supplementary motor area (SMA) degrades bimanual movement control in humans. Neurosci Lett 328:89-92

Stephan KE, Fink GR, Marshall JC (2007) Mechanisms of hemispheric specialization: insights from analyses of connectivity. Neuropsychologia 45:209-228

Tononi G, McIntosh AR, Russell DP, Edelman GM (1998) Functional clustering: identifying strongly interactive brain regions in neuroimaging data. Neuroimage 7:133-149

Varela F, Lachaux JP, Rodriguez E, Martinerie J (2001) The brainweb: phase synchronization and large-scale integration. Nat Rev Neurosci 2:229-239

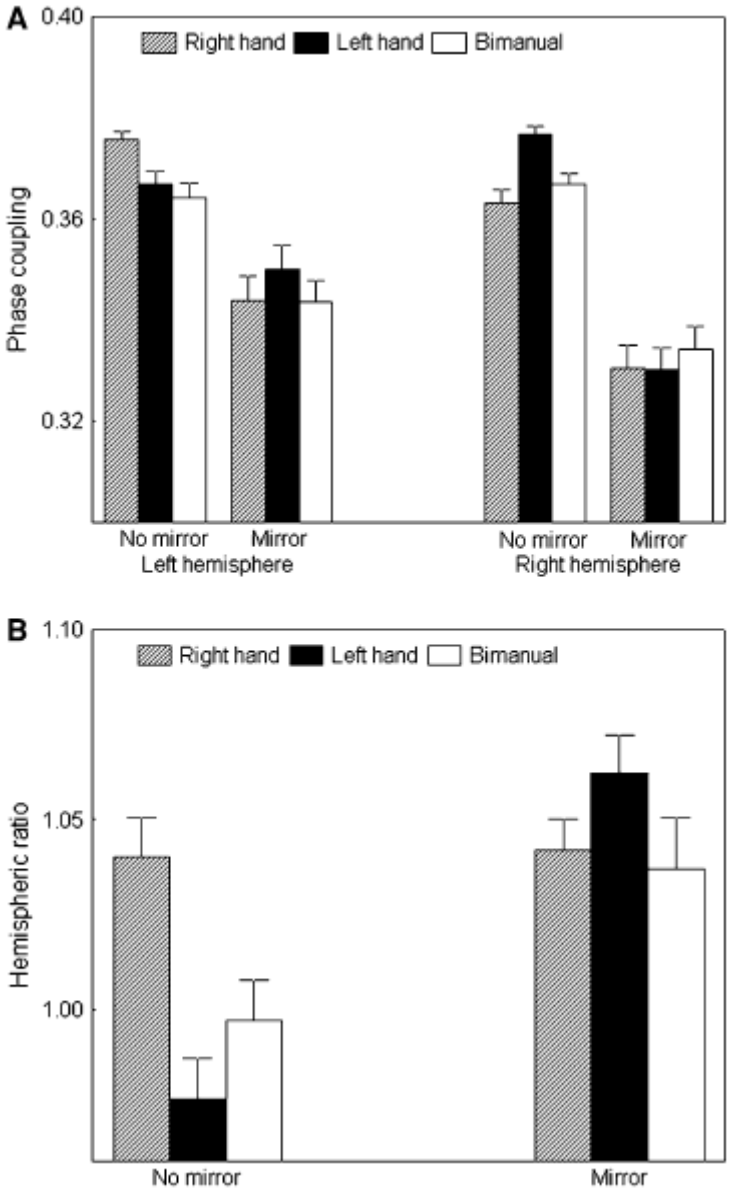
Verstynen T, Diedrichsen J, Albert N, Aparicio P, Ivry RB (2005) Ipsilateral motor cortex activity during unimanual hand movements relates to task complexity. J Neurophysiol 93:1209-1222

Wahl M, Lauterbach-Soon B, Hattingen E, Jung P, Singer O, Volz S, Klein JC, Steinmetz H, Ziemann U (2007) Human motor corpus callosum: Topography, somatotopy, and link between microstructure and function. J Neurosci 27:12132-12138

Weiss PH, Rahbari NN, Lux S, Pietrzyk U, Noth J, Fink GR (2006) Processing the spatial configuration of complex actions involves right posterior parietal cortex: An fMRI study with clinical implications. Hum Brain Mapp 27:1004-1014

Wyke M (1971) The effects of brain lesions on the performance of bilateral arm movements. Neuropsychologia 9:33-42

Fig. 1


A
0.40
0.36
0.32
Phase coupling
Right hand
Left hand
Bimanual
No mirror
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Left hemisphere
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1.10
1.05
1.00
Hemispheric ratio
Right hand
Left hand
Bimanual
No mirror
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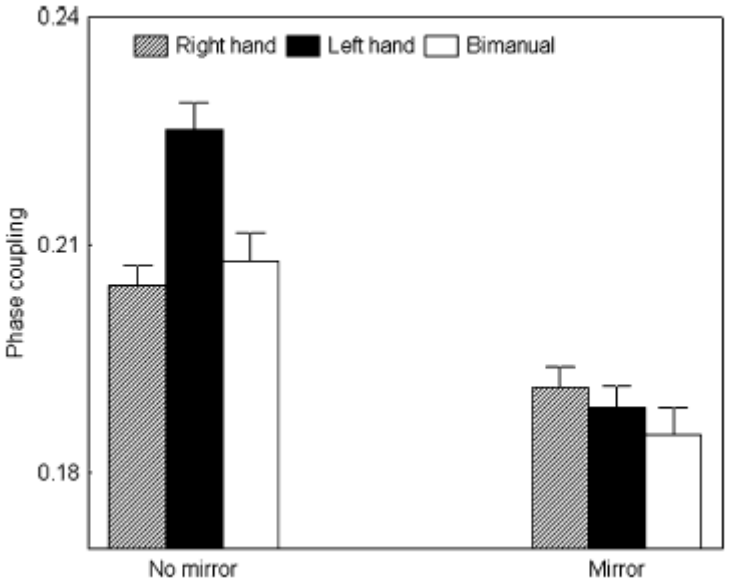
Fig. 2


0.24
0.21
0.18
Phase coupling
Right hand
Left hand
Bimanual
No mirror
Mirror